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NUMBER 9, PAGES 1-37

SEPTEMBER 25, 1972

A TAXONOMIC REVIEW OF THE SOUTHERN ANDEAN MARSUPIAL FROGS (HYLIDAE: *GASTROTHECA*)

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Marsupial frogs of the genus *Gastrotheca* are unique in their mode of reproduction and therefore are of considerable interest to biologists. Yet the taxonomy of the genus is chaotic; the nomenclature and distribution of the most common and widespread Andean species are usually erroneously reported in the literature. Consequently, in order to facilitate study of biological problems of these frogs, the basic taxonomy must be treated first.

From September 1969 through July 1970 Fritts carried out field work in the Andes of Ecuador, Perú, and Bolivia. In January 1971 both of us concentrated field work on *Gastrotheca* in central and southern Perú, and Duellman collected in Ecuador in the summer and fall of 1971. As the result of this field work we accumulated large series of *Gastrotheca* and extensive data on the ecology, life history, and distribution of several species. In the present paper we are concerned only with the species occurring in the Andes south of the Huancabamba Depression in northern Perú. We have relied mostly on our own collections and data but have studied Argentinean material provided by Raymond F. Laurent. Also, we have examined all extant type specimens of Andean *Gastrotheca* and much material in other museums.

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The purposes of the present paper are to 1) define as a natural group the marsupial frogs in the southern Andes; 2) allocate the appropriate trivial names; 3) diagnose the species and define their ranges; 4) describe two new species from the Peruvian Andes. We have examined 913 specimens from Perú, Bolivia, and Argentina. Reference to all specimens is by the abbreviations of the collections as given in the acknowledgments; the Museum of Natural History, University of Kansas is abbreviated KU.

ACKNOWLEDGMENTS

For the loan of specimens or provision of working space in their respective collections we are indebted to Nelly Carrillo de Espinosa, Museo Javier Prado, Lima (MJP); Josef Eiselt, Naturhistorisches Museum Wien (NHMW); Alice G. C. Grandison, British Museum (Natural History) (BMNH); Jean Guibé, Museum National d'Histoire Naturelle, Paris (MNHN); Walter Hellmich, Zoologische Staatssammlung München (ZSM); Konrad Klemmer, Senckenberg Museum, Frankfurt (SMF); Raymond F. Laurent, Instituto Miguel Lillo, Tucuman (IML); Alan E. Leviton, California Academy of Sciences (CAS) and Stanford University (CAS-SU); Edmond V. Malnate, Academy of Natural Sciences of Philadelphia (ANSP); Charles W. Myers, American Museum of Natural History (AMNH); Oscar Ochoa M. and Ismael Ceballos B., Museo de Zoología, Universidad Nacional San Antonio Abad, Cuzco (MZUN); James A. Peters, United States National Museum (USNM); Greta Vestergren, Naturhistoriska Riksmuseum, Stockholm (NHRM); David B. Wake, Museum of Vertebrate Zoology, Berkeley (MVZ); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); Ernest E. Williams, Museum of Comparative Zoology, Harvard (MCZ).

In 1969 and 1970 Fritts' field work was supported by a grant from the National Science Foundation (GB 8785) and in 1971 by a grant from the F. William Saul Fund, Museum of Natural History. In 1969 and 1970 Patricia R. Fritts provided valuable field assistance and companionship. Duellman received support for visits to European museums from the American Philosophical Society (Penrose Fund No. 5063). In Perú we enjoyed the hospitality and field assistance of Oscar Ochoa M. and Ismael Ceballos B. of the Universidad Nacional San Antonio Abad in Cuzco. Mr. James A. Muir of the Cerro de Pasco Mining company provided lodging and transportation. Drs. Manuel Moro, Luis Inope, Sisinio Morales Z., Efraim Gonzalez, Miguel Gallegosh, Efraim de la Vega, and Ing. Hugo Paz all assisted in logistical support of Fritts in Perú. Duellman's

travels in Ecuador were facilitated by the cooperation of Bruce MacBryde, Universidad Católica del Ecuador. We are grateful to all of these persons and institutions for making this report possible. We are indebted to Linda Trueb, who provided us with insight into some of the problems through her astute osteological observations and who executed the drawings incorporated herein. Finally we extend our gratitude to Charles F. Walker who generously shared with us his extensive knowledge of marsupial frogs.

HISTORICAL RESUMÉ

Duméril and Bibron (1841:593) named *Hyla marsupiata* from Cuzco, Perú. Their description and color illustrations could apply equally to specimens from southern Perú or from Ecuador. The holotype (MNHN 4877) is a female having a snout-vent length of 48.2 mm, 3 mm larger than any other specimen from southern Perú that we have seen, but within the size range of specimens from Quito, Ecuador. The holotype is now soft and rubbed; the color pattern is completely faded. Under the catalogue number MNHN 4878 are four small specimens from Quito, Ecuador. Jean Guibé carefully rechecked the catalogue and stated that there was no reason to suspect that the holotype was not part of the collection made in vicinity of Cuzco by Pentland. Because of the poor condition of the holotype, we could not rely on external characters for assigning it to a known population. However, radiographs revealed that the cranial characters of the holotype are like those of specimens from southern Perú and not like specimens from Ecuador. Thus, we disagree with Laurent's (1969a:129) suggestion that Vellard's (1957:19) allocation of the trivial name *marsupiata* to the population at Cuzco was erroneous.

Hyla marsupiata is the type species of *Gastrotheca* Fitzinger, 1843. Günther (1859:115) proposed the substitute generic name *Nototrema*, which was commonly used until Miranda-Ribeiro (1920:328) resurrected *Gastrotheca*.

Cope (1877:37) named *Chorophilus cuzcanus* on the basis of a specimen obtained by the Orton Expedition. Although no locality is given in the description, the specific name apparently is derived from Cuzco. The holotype cannot be found, but the description applies well to young *Gastrotheca marsupiata* from southern Perú; consequently, we consider *Chorophilus cuzcanus* Cope, 1877, to be a junior synonym of *Gastrotheca marsupiata* (Duméril and Bibron, 1841).

Steindachner (1892:840) named *Nototrema bolivianum* on the basis of six specimens from Puerto de San Mateo, Departamento

Cochabamba, Bolivia. These specimens (NHMW 16490-91) are in excellent condition; NHMW 16490, an adult female having a snout-vent length of 42.8 mm, is hereby designated as the lectotype. Thus, the five specimens catalogued under NHMW 16491 become lectoparatypes. *Hylodes caeruleomaculatus* Werner (1899:482), based on two syntypes (NHMW 16496) from "Bolivia," was placed in the synonymy of *Nototrema bolivianum* by Nieden (1923:320). The largest of the syntypes is a male having a snout-vent length of 28.8 mm. Comparison of the syntypes with the types of *N. bolivianum* and with other specimens from Bolivia and southern Perú reveals that the syntypes of *Hylodes caeruleomaculatus* are juveniles of the species earlier named *Nototrema bolivianum*.

Five syntypes (BMNH 1900.6.20-46-50) were designated by Boulenger (1900:181) in his description of *Nototrema peruanum* from "Carao" (=Caraz), Departamento Ancash, Perú. The type series consists of four adult males having snout-vent lengths of 38.3-41.5 mm and a juvenile (BMNH 1900.6.20.50) having a snout-vent length of 28.9 mm.

Thus, at the beginning of the present century three species of marsupial frogs were recognized in the genus *Nototrema* in the Andes of western South America, viz. *bolivianum*, *peruanum*, and *marsupiatum*; the latter name was used for populations in Ecuador, as well as that at Cuzco, Perú. Barbour and Noble (1920a:611) applied the name *Gastrotheca boliviana* to specimens from southern Perú and placed *Eleutherodactylus binghami* Stejneger, 1913, in the synonymy of *Gastrotheca boliviana* (Steindachner, 1892). We examined the holotype of *E. binghami* (USNM 49559), a juvenile from Cuzco, Perú, having a snout-vent length of 20.9 mm, and concur with Barbour and Noble that the specimen is a juvenile *Gastrotheca*.

Barbour and Noble (1920b:426) named *Gastrotheca monticola* from Huancabamba, Departamento Piura, Perú, and Parker (1932:25) named *Gastrotheca marsupiata lojana* from Loja, Provincia Loja, Ecuador. Shreve (1941:82) studied series of *Gastrotheca* from central Perú and concluded that they were subspecifically distinct from *G. boliviana*; he named *Gastrotheca boliviana griswoldi* from Maraynioc, Departamento Junín, Perú. The holotype (MCZ 24102) is a female having a snout-vent length of 38.6 mm.

Vellard (1957) reviewed the Peruvian marsupial frogs and recognized the following taxa in Andean Perú: *marsupiata* (two subspecies) *boliviana*, *peruana* (three subspecies), *lojana*, and *monticola*. We are not concerned here with *lojana* and *monticola*, both of which belong to the northern Andean complex of *Gastro-*

theca. Vellard (1957:22) considered *G. boliviana griswoldi* Shreve to be a synonym of *G. m. marsupiata* (Duméril and Bibron) and named *G. marsupiata bifasciata* from Paccha, Departamento Junín, Perú. Of the three syntypes of that subspecies (MJP 129), two are juveniles; the other is an adult male having a snout-vent length of 33.5 mm. Vellard named two subspecies of *G. peruana*—*G. peruana dissimilis* from Huamachuco, Departamento La Libertad, Perú, and *G. peruana junensis* from Lago de Puntún, Departamento Junín, Perú. The type series of *dissimilis* (MJP 245) contains 48 specimens, one of which is a *Telmatobius*; the holotype of *junensis* (MJP 195) is a male having a snout-vent length of 36.5 mm. Vellard's application of names to populations in central and southern Perú was influenced by his having only limited topotypic material of *G. marsupiata*, a species about which he obviously was confused.

Laurent (1967, 1969a-b) has made the most recent contributions to the systematics of southern Andean *Gastrotheca*. He named *G. christiani* from the "Monumento de la ruta de Valle Grande, 50 km de Calilegua," Provincia Jujuy, Argentina, and *G. gracilis* from La Banderita, Provincia Catamarca, Argentina. Moreover, Laurent (1969a:129) misinterpreted Vellard's (1957) allocation of *G. marsupiata*. Laurent considered *G. marsupiata bifasciata* to be a species distinct from *G. marsupiata*. He proposed the name *Gastrotheca bifasciata vellardi* for the populations in southern Perú recognized as *G. marsupiata marsupiata* by Vellard.

At the time of this writing, the taxonomy of the southern Andean *Gastrotheca* is as follows (synonyms in brackets): *G. bifasciata bifasciata* Vellard, *G. bifasciata vellardi* Laurent, *G. boliviana* (Steindachner) [*H. caeruleomaculatus* Werner, *E. binghami* Stejneger], *G. christiani* Laurent, *G. gracilis* Laurent, *G. marsupiata* (Duméril and Bibron) [*G. boliviana griswoldi* Shreve], *G. peruana peruana* (Boulenger), *G. peruana dissimilis* Vellard, and *G. peruana junensis* Vellard.

It is obvious from statements made by Barbour and Noble (1920a), Vellard (1957), and Laurent (1969a) that these authors were confused about the allocation of the specific name *marsupiata*. With the exception of Vellard, these authors and others have based their definitions of *marsupiata* on specimens from Ecuador and generally have placed all Peruvian specimens in *boliviana*, *bifasciata*, or *peruana*. Vellard (1957) assumed that Ecuadorian "*marsupiata*" were different from the nominate race at Cuzco; he proposed the name *Gastrotheca marsupiata ecuatoriensis* for Ecuadorian populations.

PROPOSED TAXONOMY

The examination of type specimens and large series of fresh specimens has provided the basis for a re-evaluation of the taxonomy of southern Andean *Gastrotheca*. Supportive data for taxonomic changes are presented here, whereas diagnoses, accounts of variation, and ranges of the recognized species are given in the accounts of the species.

The most widespread species of marsupial frog in the southern Andes is *G. marsupiata* (Duméril and Bibron). Comparison of the types of *G. marsupiata* and *G. boliviana* revealed no structural differences between the specimens. Comparison of these types with series of specimens from Bolivia and southern Perú demonstrated that many individuals, including the lectotype of *G. boliviana*, lack dorsal dark markings and have small pale spots on the dorsum. Thus, we place *G. boliviana* (Steindachner, 1892) in the synonymy of *G. marsupiata* (Duméril and Bibron, 1841). Four names (*Chorophilus cuzcanns*, Cope, 1877; *Hylodes caeruleomaculatus* Werner, 1899; *Eleutherodactylus binghami* Stejneger, 1913; *Eleutherodactylus footei* Stejneger, 1913) are based on juvenile *Gastrotheca*. We have examined the types of all but *C. cuzcanns* (type lost) and conclude that all four names are synonyms of *G. marsupiata*. Due to Laurent's (1969a) misinterpretation of Vellard's (1957) allocation of *G. marsupiata*, the substitute name *G. bifasciata vellardi* Laurent, 1969, is a synonym of *G. marsupiata*.

Vellard (1957) recognized three subspecies of *G. peruana* (Boulenger, 1900). Although certain minor differences in coloration and pustularity exist among populations of *G. peruana* throughout its range in northern and central Perú, these differences are not consistent. Thus we do not recognize subspecies of *G. peruana* and consider *G. peruana dissimilis* Vellard, 1957, and *G. peruana junensis* Vellard, 1957, to be junior synonyms of *G. peruana* (Boulenger, 1900).

Gastrotheca boliviana griswoldi Shreve, 1941, is not conspecific with *G. boliviana* (= *marsupiata*). Shreve's assignment of the population in central Perú as a subspecies of *G. boliviana* was incorrect; as a consequence, Vellard (1957) named the same population as *G. marsupiata bifasciata*. Our studies of series of specimens from Junín and Pasco and examination of the types revealed that *G. marsupiata bifasciata* Vellard, 1957, is a junior synonym of *G. griswoldi* Shreve, 1941.

Examination of limited material suggests that *G. christiani* Laurent, 1967, and *G. gracilis* Laurent, 1969, are valid species. Our

TABLE 1.—Alphabetical synonymy of species in the *Gastrotheca marsupiata* group.

Trivial Name, Original Combination, Author, Date	Current Name
<i>bifasciata</i> (<i>Gastrotheca bifasciata</i>) Vellard, 1957	<i>G. griswoldi</i>
<i>binghami</i> (<i>Eleutherodactylus</i>) Stejneger, 1913	<i>G. marsupiata</i>
<i>bolivianum</i> (<i>Nototrema</i>) Steindaehner, 1892	<i>G. marsupiata</i>
<i>caeruleomaculatus</i> (<i>Hylodes</i>) Werner, 1899	<i>G. marsupiata</i>
<i>christiani</i> (<i>Gastrotheca</i>) Laurent, 1967	<i>G. christiaui</i>
<i>cuzcanus</i> (<i>Chorophilus</i>) Cope, 1877	<i>G. marsupiata</i>
<i>dissimilis</i> (<i>Gastrotheca peruana</i>) Vellard, 1957	<i>G. peruana</i>
<i>excubitor</i> (<i>Gastrotheca</i>) new species	<i>G. excubitor</i>
<i>footei</i> (<i>Eleutherodactylus</i>) Stejneger, 1913	<i>G. marsupiata</i>
<i>gracilis</i> (<i>Gastrotheca</i>) Laurent, 1969	<i>G. gracilis</i>
<i>griswoldi</i> (<i>Gastrotheca boliviana</i>) Shreve, 1941	<i>G. griswoldi</i>
<i>juvencus</i> (<i>Gastrotheca peruana</i>) Vellard, 1957	<i>G. peruana</i>
<i>marsupiata</i> (<i>Hyla</i>) Duméril and Bibron, 1841	<i>G. marsupiata</i>
<i>ochoai</i> (<i>Gastrotheca</i>) new species	<i>G. ochoai</i>
<i>peruanum</i> (<i>Nototrema</i>) Boulenger, 1900	<i>G. peruana</i>
<i>vellardi</i> (<i>Gastrotheca bifasciata</i>) Laurent, 1969	<i>G. marsupiata</i>

own collections contain series of two additional unnamed species from Perú. Thus, we recognize seven species of *Gastrotheca* in the Andes south of the Huancabamba Depression; 16 trivial names have been proposed for these seven species (Table 1).

DEFINITION OF SPECIES GROUPS

The marsupial frogs of the southern Andes can be distinguished from those species occurring in the northern Andes and at low elevations. For ease in discussion we refer to the southern species collectively as the *Gastrotheca marsupiata* group and to the northern species as the *Gastrotheca argenteovirens* group. In the latter group we place *G. argenteovirens* (Boettger), *G. lojana* Parker, *G. monticola* Barbour and Noble, *G. plumbea* (Boulenger), and the Ecuadorian populations formerly assigned to *G. marsupiata*; the Colombian species *G. aureomaculata* Cochran and Goin and *G. mertensi* Cochran and Goin also can be associated with the *argenteovirens* group. Other species groups, such as the casque-headed species in Colombia and Venezuela and the long-legged arboreal species in the tropical lowlands, are not considered here.

The most profound difference between the *G. marsupiata* and *G. argenteovirens* groups is the nature of the frontoparietals. In both groups the frontoparietals articulate anteriorly with the dermal sphenethmoid and medially with one another. In members of the *marsupiata* group, the frontoparietals are not expanded laterally and do not extend over the otic region; a frontoparietal fontanelle

is evident. The nasals, pars facialis of the maxillary, dermal sphenethmoid, and frontoparietals are smooth in the smaller species and in small individuals of the larger species, whereas in larger individuals exostosis is evident on the frontoparietals and decreasingly so on the nasals, dermal sphenethmoid, and pars facialis of the maxillary. In members of the *argenteovirens* group the frontoparietals are expanded laterally so as to form a supraorbital flange that is broadest posteriorly; the frontoparietal fontanelle is covered with bone. In the fully developed condition in the larger species, the frontoparietals extend over the otic region and articulate with the squamosals. Exostosis is well developed on the nasals, dermal sphenethmoid, frontoparietals, and pars facialis of the maxillary; in large individuals exostosis is present on the premaxillaries and squamosals (Fig. 1).

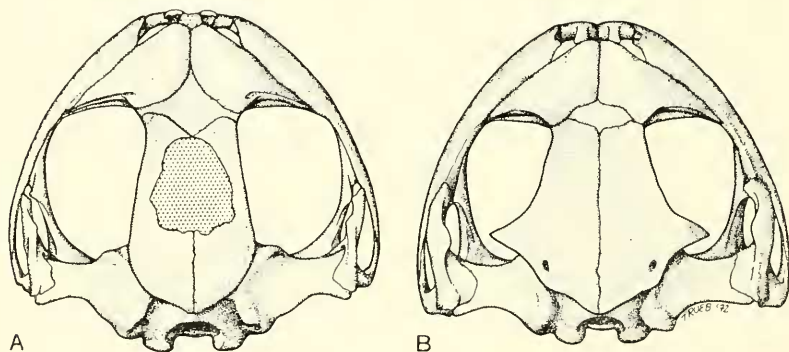


FIG. 1. Dorsal views of skulls of *Gastrotheca*. A. *G. marsupiata*, KU 138372, ♀ 14.1 mm in width. B. *G. riobambae*, KU 99128, ♀ 18.2 mm in width.

These osteological differences are closely correlated with size; larger frogs have better developed frontoparietal flanges and increased exostosis. Frogs in the *marsupiata* group are smaller than those in the *argenteovirens* group. The largest species in the *marsupiata* group is *G. peruana*, females of which attain snout-vent lengths of 53 mm, whereas females of *G. argenteovirens*, *lojana*, and *monticola* attain snout-vent lengths of 65, 68, and 77 mm, respectively.

All members of the *argenteovirens* group have free-swimming tadpoles. Three species in the *marsupiata* group have free-swimming tadpoles, but in three others development is known to be completed in the maternal pouch.

STATUS OF ECUADORIAN "*GASTROTHECA MARSUPIATA*"

Although Duméril and Bibron (1841:598) based their description of *Gastrotheca marsupiat*a on a specimen from Cuzco, Perú, the color patterns of the specimens illustrated in their atlas (Duméril and Bibron, 1854, pl. 98) suggest that the specimens probably came from Ecuador. At the time of the publication of the atlas only one specimen of *Gastrotheca marsupiat*a (the type) existed in the Paris museum; however, several Ecuadorian specimens were in the collection at that time and likely served as the basis for the illustrations. Most literature references to *Gastrotheca marsupiat*a have dealt with Ecuadorian populations. It is now evident that these populations are not conspecific with the population at Cuzco, Perú, the type locality of *G. marsupiat*a. Consequently, another name must be assigned to the Ecuadorian populations. In so doing it is desirable to point out certain problems concerning distribution and variation in the Ecuadorian populations.

We have examined 740 specimens from Ecuador and have seen approximately 250 of these alive. There is considerable variation within and between populations. The most obvious differences are in coloration and involve: 1) presence or absence of dark blotches dorsally, 2) brown versus green dorsal coloration, 3) blue or green in the groin and on the posterior surfaces of the thighs, 4) extent and color of mottling on the flanks, and 5) development of ventral spotting. In addition to differences in coloration, there are differences in size and in glandularity of the dorsal skin.

Polymorphism in dorsal color pattern (uniform versus blotched) occurs within some populations, such as those at such widely separated localities as Biblián, Guaranda, and Papallacta. Frogs from Guaranda and Papallacta are green, whether blotched or plain. Most frogs from Otavalo, Riobamba, and Quito are blotched; most specimens from Otavalo are brown. Both green and brown frogs occur at Riobamba and Quito. At the latter locality the two colors occur in about equal frequency, whereas at Riobamba brown frogs are more frequent in collections made in the dry season and green ones more common in collections made in the rainy season.

Likewise, size is highly variable. Seemingly larger individuals are found on the outer Andean slopes (Guaranda, Baños, Papallacta) than in the interandean valleys (Cuenca, Riobamba, Quito, Otavalo). Specimens from Quito are larger than those from other interandean valleys.

We have not undertaken a detailed analysis of the Ecuadorian populations, which may represent one highly variable species or

two or more species. Until such time that the Ecuadorian populations are better known and can be shown to represent more than one species, we propose that they be treated nomenclaturally as one species, *Gastrotheca riobambae* (Fowler).

Fowler (1913:157) named *Hyla riobambae* on the basis of two specimens collected at Riobamba, Provincia Chimborazo, Ecuador, by C. N. Rhoads. The holotype (ANSP 16161) is a male having a snout-vent length of 48.3 mm. The type is in good condition and obviously is a *Gastrotheca*. This is the oldest name applicable to the Ecuadorian populations formerly called *Gastrotheca marsupiata*.

Two other names apply to the same species. Fowler (1913:159) named *Hyla quitoe*, based on three juveniles from Quito, Provincia Pichincha, Ecuador. The holotype (ANSP 18235) has a snout-vent length of 18.8 mm. All three specimens are partially desiccated; no color pattern is evident, although Fowler's illustration (1913, Pl. VII) shows a pattern common in juveniles of *Gastrotheca* from Quito. Acting as first revisors, we have selected *Hyla riobambae* as having priority over *Hyla quitoe*, because: 1) *riobambae* has page priority, 2) the holotype of *riobambae* is an adult in good condition, and 3) the holotype of *quitoe* is a juvenile in poor condition.

Andersson (1945:85) named *Chorophilus olivaceus* from "Rio Napo, 400 m," Ecuador. Examination of the holotype (NHIRM 1965) reveals that it is a male *Gastrotheca* having a snout-vent length of 41.7 mm. The specimen is somewhat darkened by formalin, but a faint pattern of dark longitudinal markings is evident on the gray-brown dorsum. The flanks and thighs are plain gray except for faint dark mottling in the groin and on the distal posterior surfaces of the thighs. The type seems to be the same as *Gastrotheca riobambae*. Evidently the type locality is erroneous. The specimen was in a collection received by the Naturhistoriska Riksmuseet in Stockholm from William Clark-MacIntyre, who collected in the Pastaza valley from Baños down to the Amazon lowlands; many of his specimens came from Baños, where *Gastrotheca riobambae* is abundant. The specimen does not bear an attached original tag, so an error in recording the data is possible. The specimen probably came from the vicinity of Baños, the lowest known locality for *G. riobambae* in the Pastaza valley.

A nomenclatural summary of *Gastrotheca riobambae* follows:

***Gastrotheca riobambae* (Fowler)**

New Combination

Hyla riobambae Fowler, 1913:157 [Holotype.—ANSP 16161 from Riobamba, Provincia Chimborazo, Ecuador; S. N. Rhoads collector].

Hyla quitoe Fowler, 1913:159 [Holotype.—ANSP 18238 from Quito, Provincia Pichincha, Ecuador; S. N. Rhoads collector]. New synonymy.

Chorophilus olivaceus Andersson, 1945:85 [Holotype.—NHIRM 1965 from "Rio Napo, 400 m." (= ? Banūs, Provincia Tungurahua, Ecuador), William Clarke-MacIntyre collector]. New synonymy.

Gastrotheca m[arsupiat]a ecuatoriensis Vellard, 1957:43 [*Nomen nudum*]. New synonymy.

Distribution.—*Gastrotheca riobambae* occurs throughout the Andes, including Amazonian and Pacific slopes and interandean valleys of Ecuador from Tulcán south to the slopes of Cerro Tinajillas, Provincia Azuay. The known altitudinal range is between 1800 and 3960 m. The species probably occurs in the Andes of southern Colombia. To the south of its known range, *Gastrotheca riobambae* apparently is replaced in the Saraguro Valley by *G. monticola* and in the Loja Valley by *G. lojana*.

ACCOUNTS OF SPECIES

In the following accounts the synonymies include all names and combinations thereof applicable to a given taxon. The diagnoses are designed to distinguish the species from other *Gastrotheca* in the southern Andes. Discussions of variation deal principally with coloration, especially in life. An account of geographic and altitudinal distribution is given for each species.

Gastrotheca peruana (Boulenger)

Nototrema peruanum Boulenger, 1900:181 [Syntypes.—BMNH 1900.6.20.46-50 (RR 1947.2.22.42-46) from "Carao" (= Caraz), Departamento Ancash, Perú; P. O. Simons collector].

Gastrotheca peruana peruana—Vellard, 1957:27.

Gastrotheca peruana dissimilis Vellard, 1957:30 [Syntypes.—MJP 245 (47 specimens) from Huanchuco, Departamento La Libertad, Perú; W. Weyrauch collector]. New synonymy.

Gastrotheca peruana jimensis Vellard, 1957:33 [Holotype.—MJP 195 from Lago de Pumín, Departamento Junín, Perú; Hernando de Macedo and J. Vellard collectors]. New synonymy.

Diagnosis.—1) Snout-vent length attaining 53.8 mm in males, 52.8 mm in females; 2) snout pointed in dorsal aspect, inclined posterodorsally in profile; 3) canthus acutely rounded; 4) loreal region flat; 5) tympanum round; 6) supratympanic fold heavy, granular; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand large, round; 9) palmar tubercle large, trifold; 10) webbing absent on hand; 11) webbing present basally on foot, extending to base of antepenultimate phalange of fourth toe; 12) tarsal fold extending full length of tarsus; 13) inner metatarsal tubercles elliptical, not visible from above; 14) outer metatarsal tubercle large, round; 15) subarticular tubercles on foot large,

subconical; 16) supernumerary tubercles on foot large, conical, in one row on proximal segments; 17) discs round; 18) dorsal skin strongly granular with longitudinally ovoid tubercles; 19) dorsum predominantly gray or tan with darker gray or brown markings (with pale green centers in some individuals) consisting of pair of supraorbital marks, connected or not to pair of longitudinal blotches or series of dashes; 20) facial pattern consisting of broad, dark canthal stripe, dark postorbital mark extending from supratympanic fold to jaw and not continuous with postaxillary mark, creamy white labial stripe posterior to orbit (absent in some specimens); 21) flanks plain or with few dark flecks; 22) dorsal surfaces of limbs having broad transverse dark bars about equal in width to interspaces; 23) posterior surfaces of thighs brown with or without pale cream spots; 24) venter uniform creamy white; 25) free-swimming tadpoles.

Gastrotheca peruana can be distinguished from the other species by its pointed snout that is inclined posterodorsally in profile. Patterned individuals usually have a large spot on each eyelid (connected with dorsolateral blotch in some individuals) and no interorbital bar; these features of coloration are unique to *G. peruana*. Unpatterned individuals can be distinguished on the basis of the shape of the snout, amount of webbing, and texture of the dorsal skin.

Variation.—Adults are predominantly gray or tan with brown or green markings. An interorbital bar is always absent. The majority of specimens have a dark spot on each eyelid, connected or not with a broad, irregular, longitudinal dark mark; the longitudinal markings are continuous to the sacral region or variously fragmented (Figs. 2 A-D, 3). Most specimens have a dark blotch posterior to the sacrum. Unpatterned individuals are rare.

The following descriptions of coloration in life are excerpted from the authors' field notes.

Cajamarca, Cajamarca, 2800 m (1 specimen): "Dorsum pale gray with dark copper blotches having slight greenish suffusion in concave area of blotches, scattered dark brown flecks between blotches, smaller blotches on flanks and dorsal surfaces of thighs and shanks; canthal and postorbital stripes copper with black flecks on edges; posterior surfaces of thighs beige with pale cream tubercles; iris metallic red."

La Libertad; Huamachuco, 3350 m (7 specimens): "Adult female having golden tan dorsum with two rows of darker bronze-tan blotches outlined with yellow-green; posterior surfaces of thighs uniform beige. Adult males having yellowish green or tan

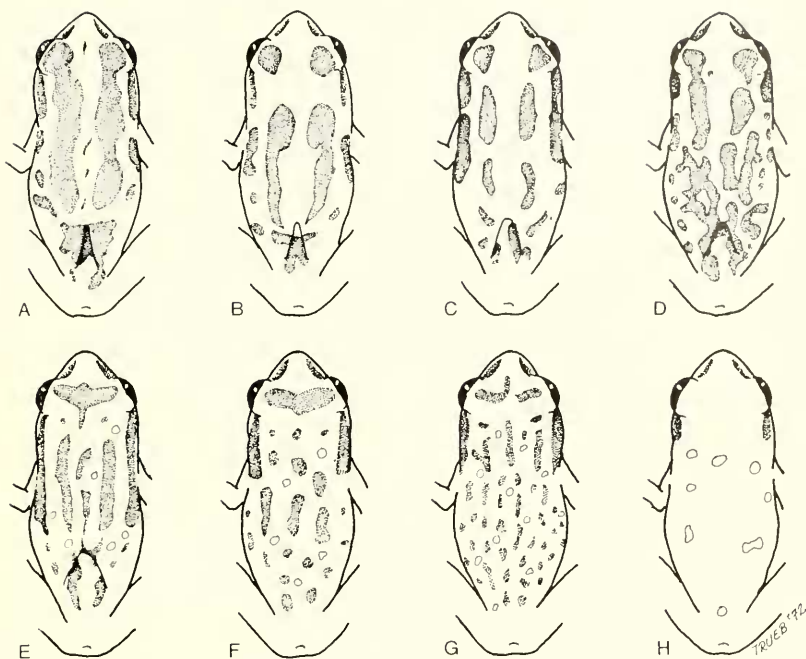


FIG. 2. Diagrammatic color patterns of *Gastrotheca peruana* (A-D) and *G. marsupiatia* (E-H).

dorsum with yellow-green or dark brown blotches; posterior surfaces of thighs and inguinal region brown with red-orange blotches. Smallest juvenile having a uniform yellow green dorsum and dull bronze-beige flanks; larger juveniles gray to yellowish tan with brown blotches; iris metallic red in adults, reddish brown in juveniles."

Ancash: 5 km N Recuay, 3450 m (18 specimens): "Dorsum gray, gray-tan, or brown in adults; one female with dorsal pattern nearly obscured by yellow-green suffusion; dorsal blotches yellow-green, yellow-tan, or brown, outlined in black; four of six adults with orange tint or orange blotches on posterior surfaces of thighs, which otherwise are dark brown with beige flecks or gray with dark brown blotches; inguinal region of adults lacking orange. Juveniles gray-beige to brown with green or dark brown blotches; posterior surfaces of thighs and inguinal region dark brown with red-orange blotches; iris red-bronze."

Huánuco: 5 km NE La Unión, 3100 m (34 specimens): "Dorsum in juveniles yellow-tan, gray-beige, yellow-green, or leaf green; most are unicolor, a few have brownish bronze or yellow-green

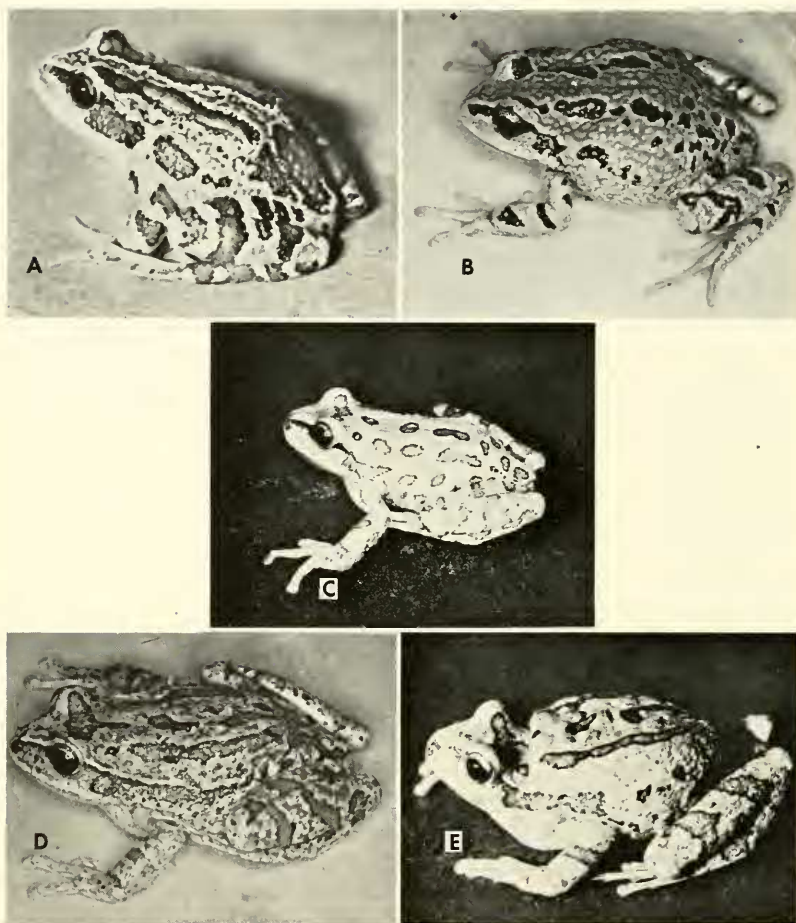


FIG. 3. A-B. *Gastrotheca peruana*. A. KU 138453, ♂ 43.0 mm in snout-vent length. B. KU 139189, ♀ 40.0 mm. C-E. *Gastrotheca marsupiata*. C. KU 139185, ♂ 33.0 mm. D. KU 139187, ♀ 43.0 mm. E. KU 138252, ♀ 43.0 mm.

blotches; smallest (<20 mm) having posterior surfaces of thighs brown with a few white flecks; those with snout-vent lengths of more than 20 mm having prominent elongate orange blotch on distal half of posterior surface of thigh and another blotch in axilla; most adults lack orange coloration; a few adults have three or four small red-orange spots on distal posterior surface of thigh; orange coloration becomes progressively fainter in larger subadults. Dorsum in adults gray, beige, or tan, all with green, tan, or brown blotches and lacking yellow spots; posterior surfaces of thighs brownish tan with white or beige flecks; iris metallic bronze."

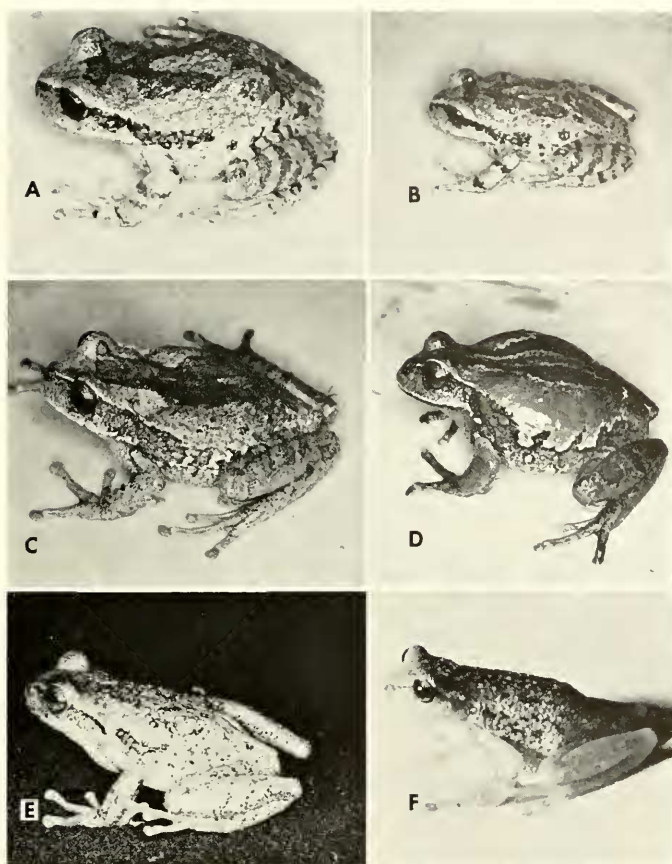


FIG. 4. A-B. *Gastrotheca griswoldi*. A. KU 139140, ♀ 37.5 mm. in snout-vent length. B. 139143, ♂ 26.5 mm. C-D. *Gastrotheca excubitor*. C. KU 139194 (holotype), ♀ 36.8 mm. D. UMMZ 131676, ♀ 41.1 mm. E-F. *Gastrotheca ochoai*. E. KU 139202 (holotype), ♀ 36.9 mm. F. KU 138666, ♀ 35.0 mm.

Junín: Between Casa Pata and Añascancha, 4050 m (2 specimens): "Dorsum tan with dark brown blotches; throat creamy yellow; belly pale gray; posterior surfaces of thighs pinkish tan; anal tubercles white; iris bronze above and copper below, with black reticulations."

It is obvious from the preceding descriptions that notable ontogenetic changes occur in color and pattern and that these changes apparently are not the same in different populations. Until the nature of the changes and the geographical limits of various populations are known, it is not feasible to recognize subspecies of *G. peruana*.

Distribution.—*Gastrotheca peruana* is wide-ranging; it extends from the Nudo de Pasco in central Perú northward to the Huanca-bamba Depression in northern Perú. The species occurs at elevations of 2300 to 3450 m on the Pacific slopes, in the valley of the Río Marañón at elevations of 2300 to 3350 m, and in the most northern headwaters of the Río Mantaro at elevations of 4000 to 4600 m (Fig. 5).

On the Pacific slopes of Perú the xeric conditions resulting from the effects of the Humboldt Current greatly affect the distribution of this species. The lower elevations recorded for the species on the Pacific slopes are in valleys protected from the desiccating



FIG. 5. Locality records for *Gastrotheca monticola* (squares), *G. ochoai* (triangles), and *G. peruana* (circles).

winds; these valleys are more moist than the exposed areas at the same elevations. The Río Chiquian near the boundary between Departamento Lima and Departamento Ancash is the southernmost Pacific valley known to be inhabited by *G. peruana*.

***Gastrotheca marsupiata* (Duméril and Bibron)**

Hyla marsupiata Duméril and Bibron, 1841:598 [Holotype.—MNHN 4877 from Cuzco, Departamento Cuzco, Perú; Pentland collector].

Nototrema marsupiatum—Günther, 1859:116.

Chorophilus cuzcanus Cope, 1877:37 [Holotype lost, named from "Perú"; James Orton collector]. New synonymy.

Nototrema bolivianum Steindachner, 1892:840 [Lectotype.—NHMW 16490 from Puerto de San Mateo, Departamento Cochabamba, Bolivia; Standiger collector]. New synonymy.

Hylodes caeruleomaculatus Werner, 1899:482 [Syntypes.—NHMW 16496 (2 specimens) from "Bolivia"; Schlüter collector]. New synonymy.

Eleutherodactylus binghami Stejneger, 1913:542 [Holotype.—USNM 49559 from Cuzco, Departamento Cuzco, Perú; obtained by Yale-Peruvian Expedition]. New synonymy.

Eleutherodactylus footi Stejneger, 1913:543 [Holotype.—USNM 49562 from Tinochehaca, Departamento Cuzco, Perú; obtained by Yale-Peruvian Expedition]. New synonymy.

Gastrotheca boliviana—Barbour and Noble, 1920a:611 [Synonymized *Eleutherodactylus binghami* Stejneger, 1913, with *Nototrema bolivianum* Steindachner, 1892].

Nototrema bolivianum—Nieden, 1923:320 [Synonymized *Hylodes caeruleomaculatus* Werner, 1899, with *Nototrema bolivianum* Steindachner, 1892].

Hylodes footi—Nieden, 1923:456.

Hylodes binghami—Nieden, 1923:456.

Gastrotheca marsupiata [*marsupiata* (by fiat)]—Parker, 1932:25.

Gastrotheca boliviana [*boliviana* (by fiat)]—Shreve, 1941:83.

Gastrotheca boliviana—Vellard, 1957:7.

Gastrotheca bifasciata vellardi Laurent, 1969a:129 [Substitute name for *Gastrotheca marsupiata marsupiata* sensu Vellard, 1957].

Diagnosis.—1) Snout-vent length attaining 41.6 mm in males, 46.5 mm in females; 2) snout acutely rounded in dorsal aspect, round in profile; 3) canthus round; 4) loreal region barely concave; 5) tympanum vertically ovoid; 6) supratympanic fold moderately heavy; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand small, subconical; 9) palmar tubercle small, trifold; 10) webbing absent on hand; 11) webbing present basally on foot, extending to base of preantepenultimate phalange of fourth toe; 12) tarsal fold extending one-third length of tarsus; 13) inner metatarsal tubercle large, elliptical, visible from above; 14) outer metatarsal tubercle small, round; 15) subarticular tubercles on foot large, conical; 16) supernumerary tubercles on foot small, round, in one row on proximal segments; 17) discs slightly wider than long; 18) dorsal skin weakly granular; 19) dorsum

green or brown, usually with dark green or dark brown markings consisting of interorbital bar or T-shaped mark not connected to longitudinal blotches or dashes on back, round cream spots or not; 20) facial pattern consisting of broad, dark canthal and postorbital stripes (latter continuous to point behind axilla) and narrow cream labial stripe; 21) flanks plain or marked with large dark spots; 22) dorsal surfaces of limbs plain or having irregular dark transverse bars; 23) posterior surfaces of thighs tan; 24) venter creamy white with or without grayish brown spots; 25) free-swimming tadpoles.

Gastrotheca marsupiata can be distinguished from the other species by the presence of an interorbital bar or T-shaped mark that is not connected to blotches or stripes on the back. Furthermore, it differs from *G. peruana* in snout shape, amount of webbing, and texture of the dorsal skin. *Gastrotheca excubitor* and *griswoldi* have an interorbital bar that usually is connected to a middorsal mark.

Variation.—The dorsal coloration is highly variable. In all large series that we have seen in life some individuals are brown and others are green. Some individuals have dark blotches and others lack blotches, whereas most individuals have some small, pale spots on the dorsum (Fig. 3). In most blotched specimens, a complete interorbital bar is present; the arrangement and size of the blotches on the dorsum vary from large dorsolateral, longitudinal blotches with smaller middorsal blotches to small longitudinal blotches over the entire dorsum (Fig. 2E-G).

Variation in living individuals is documented by descriptions excerpted from Fritts' field notes:

Huancavelica: Huancavelica, 3780 m (12 specimens): "One male uniform brown; one male yellowish tan with numerous yellow spots; six adults pale brown with olive-green to leaf green dorsal blotches; most of latter six with a few yellow spots on dorsum; two females and one male grayish brown with olive-green blotches; posterior surfaces of thighs pale brown to grayish brown with white flecks; dorsal and anterior surfaces of thighs pinkish beige with brown or dark green bars; iris metallic bronze, occasional specimens with yellow line over pupil. One juvenile golden brown with olive-green blotches."

Huancavelica: 10 km W Lircay, 3700 m (30 specimens): "Majority are grayish beige ground color; approximately one-third are yellow-beige; dorsal blotches olive-green to grayish brown; four juveniles uniform gray; all adults of both sexes having few to many yellow spots dorsally; posterior surfaces of thighs gray

with white tubercles; all blotched individuals have a T or transverse bar between orbits; all uniform gray individuals have narrow, slightly gray bars on dorsal surfaces of thighs; iris metallic bronze."

Cuzco: 10 km E Abra Huillque, 3700 m (8 specimens): "Dorsum gray-beige to bronze-beige; all adults, except one female, have numerous yellow spots on dorsum; one male without dorsal blotches; one male with faint green dorsal blotches; one male with bronze dorsal blotches; other adults have leaf green dorsal blotches; one juvenile with uniform yellow-green dorsum."

Cuzco: 4 km NW Cuzco, 3600 m (36 specimens): "Dorsum gray-beige to medium brown; most individuals have yellow-green blotches often outlined with narrow black line; most adults and some subadults have small to large yellow spots on head, body, and thighs; approximately one-third of individuals are unicolor dorsally, except for yellow spots; unicolor adults tan, some with yellow suffusion; juveniles uniformly yellowish green; venter grayish white; posterior surfaces of thighs dark tan with white tubercles; iris metallic bronze."

Cuzco: Sicuani, 3530 m (12 specimens): "Dorsum pale to dark gray-beige with extensive bronze suffusion in adults and slight bronze suffusion in smaller individuals; all but two have yellow-green blotches outlined with narrow black line; one individual having pale green blotches and one lacking blotches; dorsal surfaces of thighs gray-beige with yellow-green bars; most larger individuals with numerous pale yellow spots on dorsum; posterior surfaces of thighs pale brown with numerous white tubercles; iris metallic bronze."

Cuzco: Granja de la Raya, 4250 m (13 specimens): "Dorsum gray, gray-beige, or medium brown; approximately one-third of individuals have intense green suffusion over entire dorsum, most prominent on anterior half of body; all have yellow-green blotches outlined with narrow black line and pale to bright yellow spots on dorsum and thighs; posterior surfaces of thighs pale greenish beige with white tubercles; iris metallic bronze."

Distribution.—*Gastrotheca marsupiata* is known from the Nudo de Pasco in central Perú to southern Bolivia (Fig. 6). The species is known from elevations of 2760 to 4360 m in the Peruvian river valleys of the Río Mantaro, Río Apurímac, and Río Urubamba and the altiplano of Lago Titicaca. In Bolivia it is known from the eastern slopes of Departamento La Paz southward to Departamento Chuquisaca. Little altitudinal data exists for Bolivian specimens; however, Hans Hoffman (pers. com.) observed individuals

of *Gastrotheca marsupiata* at 2560 m in the city of Cochabamba. The species occurs at La Paz at an elevation of 3700 m.

Although populations of *G. marsupiata* and *G. griswoldi* are known from geographically close localities in the upper Río Mantaro valley, the two species have not been found in sympatry. *Gastrotheca marsupiata* is not known to occur above 3600 m near the Nudo de Pasco, although it is known at higher elevations in other parts of its range. Similarly, *G. griswoldi* occurs at elevations of 3200 to 3700 m in other parts of its range, but in the upper Río Mantaro valley it is known only from localities at 3700 m or higher. Present information indicates that a parapatric relationship exists between *G. marsupiata* and *G. griswoldi*.

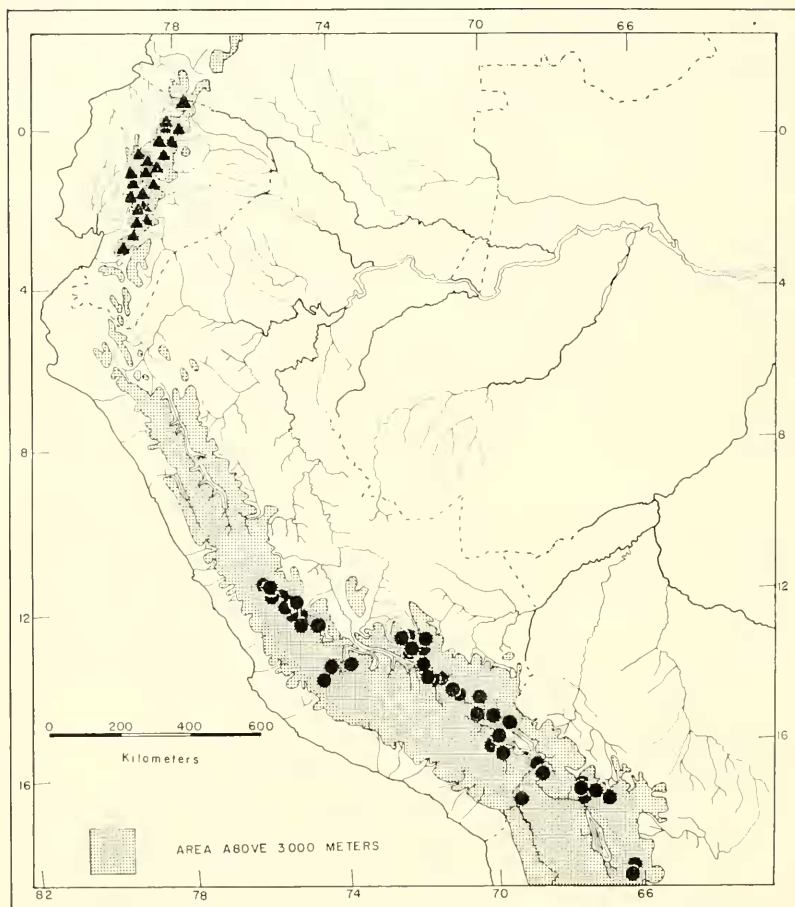


FIG. 6. Locality records for *Gastrotheca marsupiata* (circles) and *G. rio-bambae* (triangles).

***Gastrotheca griswoldi* Shreve**

New Combination

Gastrotheca boliviana griswoldi Shreve, 1941:83 [Holotype.—MCZ 24102 from Maraynioc, Departamento Junín, Perú; J. A. Griswold collector].

Gastrotheca marsupiata bifasciata Vellard, 1957:23 [Syntypes.—MJP 129 (3 specimens) from Paccha, near Lo Oroya, Departamento Junín, Perú; Jehann Vellard collector]. New synonymy.

Gastrotheca bifasciata bifasciata—Laurent, 1969a:131.

Diagnosis.—1) Snout-vent length attaining 37.8 mm in males, 44.0 mm in females; 2) snout round in dorsal aspects and in profile; 3) canthus round; 4) loreal region barely concave; 5) tympanum round; 6) supratympanic fold heavy, granular; 7) subarticular tubercles on hand large, subconical; 8) supernumerary tubercles on hand large, conical; 9) palmar tubercle large, trifold; 10) webbing absent on hand; 11) webbing present basally on foot, extending to base of preantepenultimate phalange of fourth toe; 12) tarsal fold extending one-half length of tarsus; 13) inner metatarsal tubercle elongate, visible from above; 14) outer metatarsal tubercle small, conical; 15) subarticular tubercles on foot large, round; 16) supernumerary tubercles on foot large, conical, in one row on proximal and medial segments; 17) discs nearly round; 18) dorsal skin smooth to weakly granular; 19) dorsum green, gray, or tan with darker markings consisting of interorbital bar with narrow connection to diverging, irregular longitudinal marks on back; 20) facial pattern consisting of broad canthal and postorbital stripes (latter continuous to point behind axilla) and narrow cream labial stripe; 21) flanks plain or marked with few small dark spots; 22) dorsal surfaces of limbs having narrow transverse dark bars; 23) posterior surfaces of thighs pale brown; 24) venter creamy white with or without few small brown spots; 25) metamorphosis completed within maternal pouch.

Gastrotheca griswoldi differs from all other species, except *G. gracilis* and *excubitor*, in having a dark interorbital bar connected medially to the dorsal markings. In *G. griswoldi* the dorsal markings are narrow and divergent, whereas in *G. excubitor* the markings are broad, parallel, and in some individuals fused. In *G. gracilis* the interorbital bar is connected with a middorsal stripe. *Gastrotheca griswoldi* further differs from *G. excubitor* by having a heavier supratympanic fold, larger supernumerary tubercles, less webbing, and a large trifold, instead of small bifid, palmar tubercle. *Gastrotheca griswoldi* also differs from *G. gracilis* by having a broader, more rounded snout in dorsal aspect, less webbing, larger supernumerary tubercles on the foot, and round, instead of truncate, discs.

Variation.—The most noticeable variation is in dorsal color pattern (Fig. 7A-D). Of ten adults from Maraynioc, Perú, three have pattern A, six pattern B, and one pattern C. The variation in 11 adults from Paccha, Perú, is eight B and three C, whereas in 10 adults from Comas, Perú, the variation is eight B, one C, and one D. Of four adults from 14 km SW of Paucartambo, Perú, three have pattern B, and one has pattern D, but two of the individuals with pattern B have very faint patterns on a grayish tan dorsum bearing diffuse orange blotches.

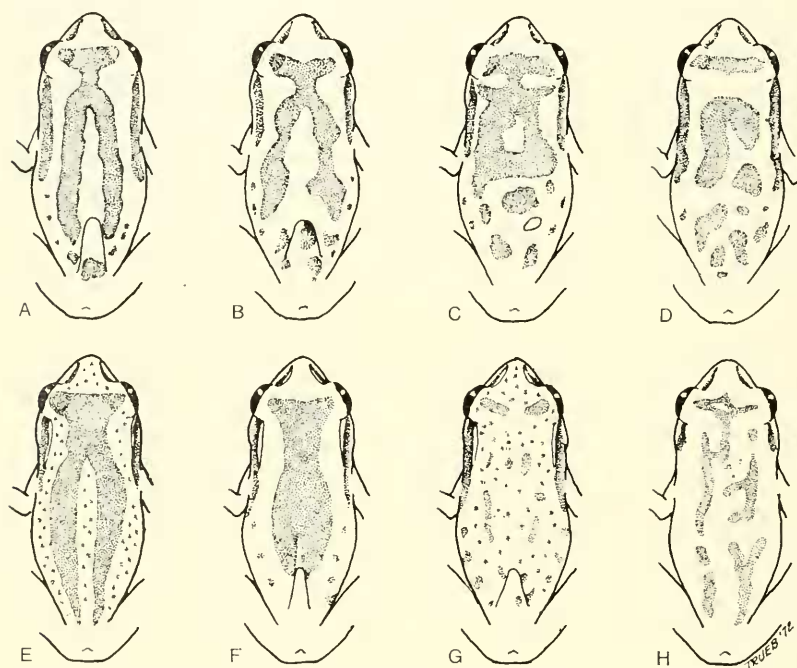


FIG. 7. Diagrammatic color patterns of *Gastrotheca griseoidi* (A-D), *G. excubitor* (E-G), and *G. gracilis* (H).

In life, individuals from Paccha were gray or tan with brown or green markings; some individuals also had yellow or orange spots on the dorsum (Fig. 4). In specimens from Comas, the spots were dull red. The venter was creamy white with or without black flecks, and the flanks were gray with black or green spots. The iris was dull bronze, darkest (nearly copper) ventrally, with a median horizontal red-brown streak and black reticulations. Two individuals from 14 km SW of Paucartambo, Perú, were colored like those from Paccha, but one individual was grayish tan with

dark green markings narrowly outlined with cream. Juveniles having snout-vent lengths of less than 20 mm have uniformly green dorsal coloration in life.

Distribution.—*Gastrotheca griswoldi* is known from elevations between 3700 and 3800 m in the northern Río Mantaro valley and from elevations of 3200 to 3700 m on the eastern slopes of the Andes in central Perú in the valleys forming the headwaters of the Río Perené (Fig. 8). Vellard (1957:25) recorded eight specimens (MJP 494) from "Caina cerca de Huánuco, 3600 mts.," Departamento Huánuco, Perú. We have examined six specimens (MJP 494) bearing a locality label "Huánuco." The city of Huánuco, because of its low elevation and xeric climate, is a doubtful locality for *G. griswoldi*, but Caina at 3600 m may support a population of the species. If the locality given by Vellard is correct, these specimens represent the only population known from the northern slopes of the Nudo de Pasco or the Río Huallaga drainage.

The distribution of *G. griswoldi* on the southern slopes of the Nudo de Pasco in central Perú approaches the ranges of *G. marsupiat*a and *G. peruana*. The three species occur in the short distance (less than 80 km) between Jauja and Carhuamayo. *Gastrotheca marsupiat*a is known from elevations of 3400 to 3600 m near Jauja (Vellard, 1957); *G. griswoldi* occurs near La Oroya at elevations of 3700 to 3800 m, whereas *G. peruana* is known from elevations of 4000 to 4600 m near Junín and Carhuamayo. No two of the three species have been found in sympatry.

Gastrotheca excubitor new species

Holotype.—KU 139194, adult female, from the northern slope of Abra Acanacu, 31 kilometers (by road) north-northeast of Paucartambo, Departamento Cuzco, Perú, 3370 m; one of a series obtained on 16 January 1971 by William E. Duellman, Thomas H. Fritts, and Oscar Ochoa M.

Paratypes.—KU 139195-97, same data as holotype; KU 139193 from 3270 m on north slope of Abra Acanacu; KU 139198 from 3400 m on north slope of Abra Acanacu; KU 139199-201, UMMZ 131676, IML 2014 from the crest of Abra Acanacu, 3520 m.

Diagnosis.—1) Snout-vent length attaining 39.5 mm in males, 41.1 mm in females; 2) snout round in dorsal aspect and in profile; 3) canthus acutely rounded; 4) loreal region barely concave; 5) tympanum vertically ovoid; 6) supratympanic fold weak, granular; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand small, subconical; 9) palmar tubercle small, bifid; 10) webbing absent on hand; 11) webbing present basally on

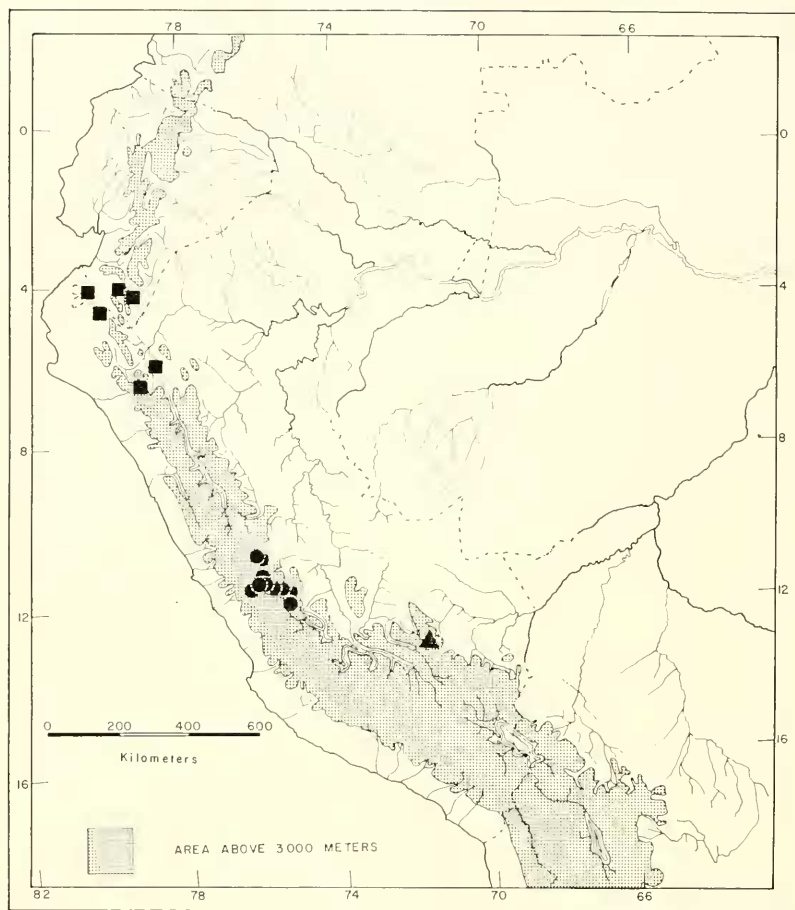


FIG. 8. Locality records for *Gastrotheca excubitor* (triangle), *G. griswoldi* (circles), and *G. lojana* (squares).

foot, extending to base of antepenultimate phalange of fourth toe; 12) tarsal fold extending one-fourth length of tarsus; 13) inner metatarsal tubercle elliptical, visible from above; 14) outer metatarsal tubercle small, round; 15) subarticular tubercles on foot large, conical; 16) supernumerary tubercles on foot small, conical, in one row on proximal segments; 17) discs nearly round; 18) dorsal skin smooth; 19) dorsum tan, gray, or green with dark brown or green markings consisting of broad interorbital bar connected to pair of broad, longitudinal stripes, partly or completely coalesced in some specimens; 20) facial pattern consisting of broad, dark canthal and postorbital stripes, bordered above by narrow

light stripes, and pale labial stripe; 21) flanks tan, green, or gray with large dark spots; 22) dorsal surfaces of limbs having narrow transverse dark bars; 23) posterior surfaces of thighs dark brown; 24) venter tan with brown spots; vocal sac gray; 25) metamorphosis presumably completed in maternal pouch.

Gastrotheca excubitor has an interorbital bar connected with the dorsal markings; in this way it differs from all other species, except *G. griswoldi* and *G. gracilis*. In *G. excubitor* the dorsal markings are broad and parallel, whereas in *G. griswoldi* the markings are narrow and divergent posterolaterally, and in *G. gracilis* the interorbital bar is connected to a middorsal stripe. *Gastrotheca excubitor* further differs from both *G. griswoldi* and *gracilis* by having smaller supernumerary tubercles on the hand, a weaker supratympanic fold, and a small bifid, instead of large trifid, palmar tubercle.

Variation.—Measurements and proportions of four adult males are followed by those of five adult females (means in parentheses): snout-vent length 33.9-39.5 (36.0), 35.1-41.1 (37.1) mm; tibia/snout-vent 0.471-0.500 (0.484), 0.482-0.527 (0.510); foot/snout-vent 0.435-0.497 (0.473), 0.465-0.544 (0.491); head length/snout-vent 0.316-0.351 (0.334), 0.332-0.353 (0.342); head width/snout-vent 0.354-0.383 (0.365), 0.350-0.389 (0.378); interorbital distance/head width 0.267-0.329 (0.303), 0.266-0.335 (0.302); tympanum/eye 0.378-0.540 (0.469), 0.459-0.593 (0.503).

Although there is considerable variation in color, the dorsal pattern is rather constant in most individuals (Fig. 7E-G). Of 11 adults from Abra Acanacu, eight are pattern E, two are F, and one is G. In life, seven individuals had a tan dorsum with brown markings; three were green with dark green markings, and one was reddish brown with dark brown markings (Fig. 4). In some individuals the dorsal dark markings are narrowly outlined with bronze-tan, but all specimens have a narrow bronze-tan stripe bordering the upper edges of the canthal and postorbital stripes. In one specimen the postorbital dark stripe and bordering bronze-tan stripe are continuous to the groin, although the stripes have an irregular upper border and indistinct lower border.

In life, the flanks are bronze-tan to bluish green with dark brown and/or cream spots. The venter is tan, and in calling males the vocal sac is dark gray. The iris is copper with fine black reticulations. A juvenile having a snout-vent length of 16.3 mm was colored like the adults with a tan dorsum with dark brown markings.

Distribution.—*Gastrotheca excubitor* is known only from ele-

variations of 3270 to 3520 m on the crest and northern slope of Abra Acanacu, Departamento Cuzco, Perú (Fig. 8). All localities are in wet páramo along the Paucartambo-Pilcopata road. Abra Acanacu is a pass in the Cadena del Paucartambo, the northwestern part of the Cordillera Carabaya. The Cadena del Paucartambo is the divide between the drainage systems of the Río Ucayali and the Río Madre de Dios. The southwestern slopes of the Cadena del Paucartambo are drained by the Río Paucartambo, which flows northward through a dry valley in the rain shadow of the cordillera, into the Río Urubamba, a southern tributary of the Río Ucayali, a large tributary of the Río Amazonas. The northeastern slopes of the Cadena del Paucartambo receive prevailing moist winds and are drained by the Río Cozñipata and Río Pilcopata, tributaries of the Río Alto Madre de Dios.

Etymology.—The specific name is Latin meaning sentinel, in reference to the outlying Cadena del Paucartambo, the type locality.

Gastrotheca gracilis Laurent

Gastrotheca gracilis Laurent, 1969b:146 [Holotype.—IML 1389 from La Banderita, Kilometer 51, Ruta Concepción-Andalgalá, Provincia Catamarca, Argentina; Roberto Ceí collector].

Diagnosis.—1) Snout-vent length attaining 37.1 mm in males, 48.0 in females; 2) snout acutely rounded in dorsal aspect, round in profile; 3) canthus round; 4) loreal region barely concave; 5) tympanum round; 6) supratympanic fold moderately heavy; 7) subarticular tubercles on hand large, round; 8) supranumerary tubercles on hand large, conical; 9) palmar tubercle large, trifid; 10) webbing absent on hand; 11) webbing present basally on foot, extending to base of antepenultimate phalange of fourth toe; 12) tarsal fold extending one-fourth length of tarsus; 13) inner metatarsal tubercle elongate, visible from above; 14) outer metatarsal tubercle small, round; 15) subarticular tubercles on foot large, conical; 16) supernumerary tubercles on foot small, subconical; 17) discs broadly ovid, roundly truncate; 18) dorsal skin bearing small, low tubercles; 19) dorsum gray with green markings consisting of interorbital T-shaped mark connected to middorsal stripe, pair of dorsolateral stripes (continuous or fragmented); 20) facial pattern consisting of narrow, dark canthal and postorbital stripes and narrow tan labial stripe; 21) flanks pale gray with dark spots; 22) dorsal surfaces of limbs with broad dark transverse bars; 23) posterior surfaces of thighs gray; 24) venter creamy white with brown spots; 25) free-swimming tadpoles.

Gastrotheca gracilis has an interorbital bar connected to a mid-

dorsal stripe, bordered on either side by dorsolateral dark stripes that are continuous or fragmented. The only other species having an interorbital bar connected to dorsal markings are *G. griswoldi* and *excubitor*; in these species there is no middorsal stripe, but rather a pair of longitudinal marks. *Gastrotheca gracilis* also differs from those species by having an acutely rounded snout in dorsal aspect, instead of a broad, round snout. *Gastrotheca gracilis* further differs from *G. griswoldi* by having more webbing, smaller supernumerary tubercles on the foot, and broader, truncate discs, and from *G. excubitor* by having larger supernumerary tubercles on the hand, a heavier supratympanic fold, and a large trifold, instead of a small bifid, palmar tubercle.

Variation.—Snout-vent lengths of five adult males from the type locality are 34.9–37.1 (mean 35.8) mm; the largest adult female has a snout-vent length of 48 mm. We have not seen living individuals of this species; the following description is a free translation of Laurent (1969b:147): “Color in life gray with green lines or blotches (blotches turn blue in formalin), which form an irregular more or less reticulated pattern on the back and limbs, with a tendency to be arranged in three longitudinal lines anteriorly and a subcanthal zone that extends from the tip of the snout to the shoulder, passing below the eye and around the tympanum, which is dark brown.”

In preservative, four males are brown, and one is gray. All have three rows of interrupted longitudinal marks on the back, the middorsal stripe beginning with a T-shaped mark between the eyes and extending to the sacral region. The dorsolateral stripes extend from the nape to the anus (Fig. 9). There are three dark diagonal bars on each thigh and shank and two on each forearm. A dark brown canthal-postorbital stripe is fragmented into irregular dark spots on the creamy tan flanks. The labial stripe is indistinct, narrow, and tan. The throat is brown, and the chest and belly are cream with small brown spots.

Distribution.—*Gastrotheca gracilis* is known from elevations of 1500 to 2000 m in the Sierra del Aronquija, an eastern spur of the Andes in northern Argentina.

Gastrotheca ochoai new species

Holotype.—KU 139202, adult female, from southwest base of Cordillera de Vilcanota, west of Río Runtumayo, about 3 kilometers north of Chilca, 10 kilometers (by road) northwest of Ollantaytambo, Departamento Cuzco, Perú, 2760 m; one of a series obtained on 9 January 1971 by William E. Duellman and Thomas H. Fritts.

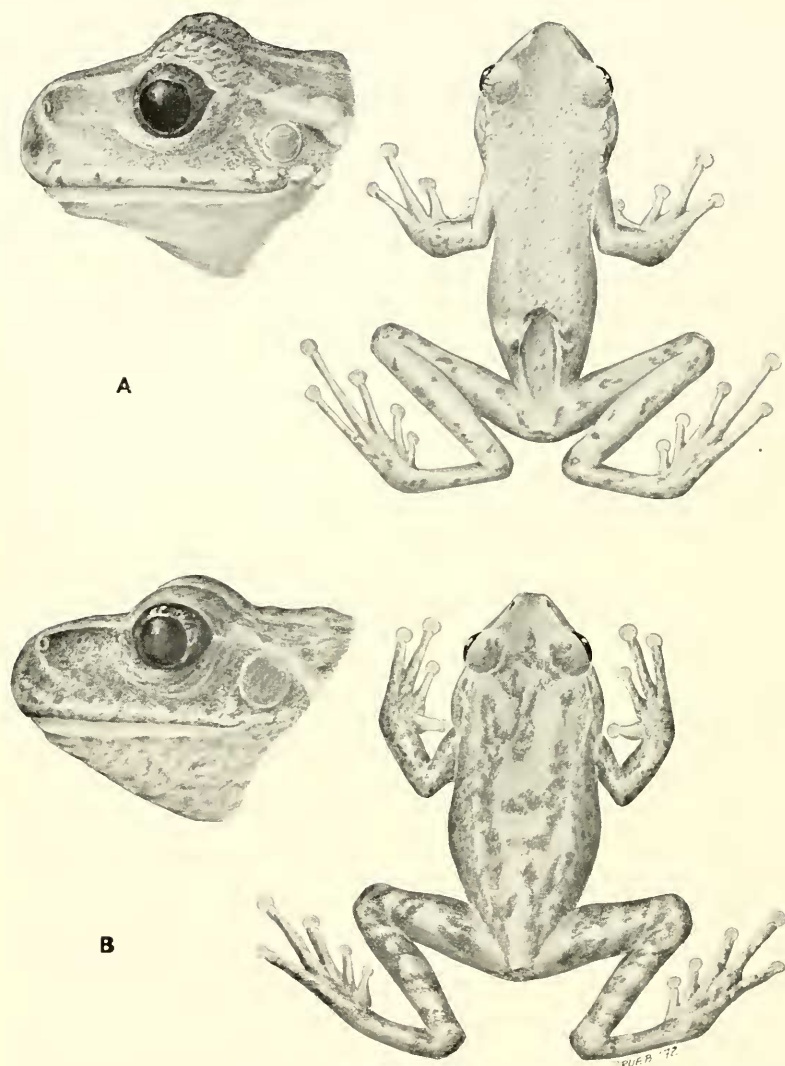


FIG. 9. A. *Gastrotheca christiani*, IML 1606, ♀ 40.0 mm in snout-vent length. B. *Gastrotheca gracilis*, IML 1530, ♂ 36.0 mm.

Paratopotypes.—IML 2012, KU 138631-35, 138645-58, 139203-09, UMMZ 131688 (9).

Diagnosis.—1) Snout-vent length attaining 32.9 mm in males, 37.9 mm in females; 2) snout pointed in dorsal aspect, round in profile; 3) canthus round; 4) loreal region barely concave; 5) tympanum round; 6) supratympanic fold weak, granular; 7) sub-articular tubercles on hand large, round; 8) supernumerary tu-

bercles on hand large, round; 9) palmar tubercle large, bifid; 10) webbing absent on hand; 11) webbing present basally on foot, extending to middle of preantepenultimate phalange of fourth toe; 12) tarsal fold absent; 13) inner metatarsal tubercle elongate, visible from above; 14) outer metatarsal tubercle large, round; 15) subarticular tubercles on foot large, subconical; 16) supernumerary tubercles on foot small, round, in one row on proximal segments; 17) discs wide, roundly truncate; 18) dorsal skin bearing small tubercles; 19) dorsum tan with dark flecks and (in some individuals) median or pair of longitudinal brown blotches; 20) facial pattern consisting of narrow, dark brown canthal and postorbital stripes and tan lips; 21) flanks tan with or without dark flecks; 22) dorsal surfaces of limbs tan with dark flecks; 23) posterior surfaces of thighs pale brown; 24) venter dusky white; 25) metamorphosis completed in maternal pouch.

Gastrotheca ochoai differs from all other species, except *G. christiani*, in having a pointed snout in dorsal aspect and round in profile, and in lacking a tarsal fold and labial stripe. *Gastrotheca ochoai* can be distinguished from *G. christiani* by the following (characters of *G. christiani* in parentheses): supratympanic fold weak (shelf-like), palmar tubercle bifid (elongate, single), no webbing on hand (fingers webbed basally), dorsal skin bearing small, round tubercles (large ovoid tubercles), no dark interorbital mark (interorbital bar or T-shaped mark), and venter dusky (spotted).

Variation.—Measurements and proportions of 12 topotypic adult males are followed by those of 10 females (means in parentheses): snout-vent length 25.9-29.2 (27.9), 30.8-36.9 (33.4) mm; tibia/snout-vent 0.490-0.580 (0.530), 0.489-0.559 (0.527); foot/snout-vent 0.430-0.495 (0.455), 0.422-0.489 (0.452); head length/snout-vent 0.330-0.355 (0.342), 0.321-0.364 (0.333); head width/snout-vent 0.344-0.381 (0.368), 0.336-0.364 (0.351); interorbital distance/head width 0.206-0.344 (0.298), 0.264-0.319 (0.303); tympanum/eye 0.355-0.640 (0.441), 0.429-0.613 (0.522).

The following coloration in life of the holotype is taken from Duellman's field notes: "Dorsum golden tan with scattered fine brown flecks; side of head bronze; canthal and postorbital stripes dark brown; flanks and dorsal surfaces of limbs bronze-tan with black flecks; venter dusky white; ventral surfaces of limbs slightly darker; tympanum dark brown; iris deep bronze with black reticulations."

In life, all adults are golden tan with black or brown markings (Fig. 4). In some individuals from Chilca there is a distinct greenish tint on the head, whereas in individuals from Ollachea,

Departamento Puno, Perú, there is a rusty red tint on the head in males and subadult females. In adult females from Ollachea the flanks are brown with a greenish tint. In many preserved specimens an irregular middorsal brown blotch or a pair of blotches are present. In life, the frogs are capable of changing from golden tan to brown and can develop more intense dorsal patterns. Apparently the blotches are formed by expansion of melanophores; subsequent contraction of melanophores results in a flecked dorsal pattern.

Young removed from the pouches of females were dull gray with a black canthal stripe. The coloration of juveniles having snout-vent lengths of 13-15 mm is more like that of the adults. The dorsum is golden beige with small brown flecks; the canthus is dark brown grading ventrally to a golden tan lip. The upper arm is yellow, and the postorbital stripe is dark brown. The dorsal surfaces of the thighs are golden yellow with a few yellow spots; the posterior surfaces of the thighs are golden with small brown flecks and a few small, bright yellow spots around the anus. The axillary region is transparent, and the venter is white with a greenish blue tint. The iris is bronze.

Distribution.—*Gastrotheca ochoai* is known from three localities on the northeastern slopes of the Cordillera de Carabaya and on the southwestern slope of the Cordillera de Vilcanota in the valley of the Río Urubamba (Fig. 5). All specimens have been found in terrestrial bromeliads at elevations of 2760 to 2800 m.

Etymology.—The patronym is for Prof. Oscar Ochoa M. of the Departamento de Biología, Universidad Nacional San Antonio Abad, Cuzco, who provided facilities at his home at Hacienda Chilea and aided in collecting specimens.

Gastrotheca christiani Laurent

Gastrotheca christiani Laurent, 1967:354 [Holotype.—IML 1369 from Monumento Ruta Valle Grande, 50 kilometers northwest of Calilegua, Provincia Jujuy, Argentina; Christian Halloy collector].

Diagnosis.—1) Snout-vent length attaining 34.0 mm in males, 40 mm in females; 2) snout acutely rounded in dorsal aspect, round in profile; 3) canthus sharply rounded; 4) loreal region concave; 5) tympanum round; 6) supratympanic fold shelf-like, granular; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand large, round; 9) palmar tubercle large, elongate, single; 10) webbing present basally between fingers; 11) webbing present basally on foot, extending to middle of antepenultimate phalange of fourth toe; 12) tarsal fold absent; 13) inner metatarsal tubercle large, elongate, broadly visible from above; 14) outer metatarsal

tubercle small, conical; 15) subarticular tubercles on foot large, subconical; 16) supernumerary tubercles on foot small, round, in one row on proximal segments; 17) discs broad, roundly truncate; 18) dorsal skin bearing ovoid longitudinal tubercles; 19) dorsum gray or brown with darker markings consisting of interorbital bar or T-shaped mark and irregular longitudinal marks on back; 20) facial pattern consisting of narrow dark canthal and postorbital stripes and brown spots on lips; 21) flanks tan with small irregular brown spots; 22) dorsal surfaces of limbs tan with small brown spots or narrow transverse bars; 23) posterior surfaces of thighs brown; 24) venter creamy white with many small dark spots; 25) metamorphosis completed in maternal pouch.

Gastrotheca christiani resembles *G. ochoai* in having a pointed snout in dorsal aspect and round in profile, and in lacking a tarsal fold and labial stripe. In these characters *G. christiani* and *ochoai* differ from all of the other species. *Gastrotheca christiani* differs from *G. ochoai* as follows (characters of *G. ochoai* in parentheses): supratympanic fold shelf-like (weak), palmar tubercle single, elongate (bifid), fingers webbed basally (no webbing), dorsal skin bearing ovoid tubercles (small, round tubercles), interorbital bar or T-shaped mark (no interorbital mark), and venter spotted (dusky).

Variation.—We have not seen living individuals of this species, so we present a free translation of Laurent's (1969a:128) description: "Color in life gray to brown with a few darker markings. In the holotype, the paratypes, and one of the males, the blotches are large. Moreover they have a characteristic form and pattern: a transverse bar or a T between the eyelids, two dorsolateral bands separated from the interocular mark. In the other specimens the dark markings are scarce, small, and irregular. A dark band extends from the nostril to the inguinal region; in places the band has many pale vermiculations. The venter is pale with many small dark blotches, most numerous on the throat and chest."

In preservative, one adult female is brown with a dark brown postorbital stripe fragmented into irregular spots on the grayish tan flanks. A broadly interrupted dorsolateral row of small, irregular, brownish black spots extends from the inner edge of the eyelid to the anus. The lips are tan with small brown spots. The limbs are brown with small dark brown spots (Fig. 9).

Distribution.—*Gastrotheca christiani* is known only from 2600 m in the Serranía de Calilegua, a part of the eastern slope of the Andes in Departamento Jujuy in extreme northern Argentina.

DISCUSSION

Comparison of the ecological aspects of the species in the *Gastrotheca marsupiata* group is limited by the paucity of available data. Most of the following discussion is based on our own observations. *Gastrotheca excubitor* occupies high, moist páramo and elfin woodland on the eastern Andean crest. *Gastrotheca ochoai* has been found only in terrestrial bromeliads at intermediate elevations (2760-2800 m) in Amazonian and interandean valleys; the species occurs in a transition zone between montane páramo and low montane forest. All localities from which it is known have scattered woody shrubs and extensive grassy areas (Fig. 10). The species of bromeliad inhabited by *G. ochoai* occurs in trees and on cliffs at elevations of 2000 to 3000 m in the Río Urubamba valleys (Figs. 11-12). Possibly the range of *G. ochoai* extends down the valley into the upper montane forest.

In the Río Urubamba valley *G. ochoai* occurs in sympatry with *G. marsupiata*. In the former the young metamorphose within the maternal pouch, whereas young of *G. marsupiata* have prolonged development as free-swimming tadpoles prior to metamorphosis. The distribution of *G. excubitor* closely approaches that



FIG. 10. Valley of the Río Urubamba north of Chilca, Departamento Cuzco, Perú, with the southwestern base of the Cordillera de Vilcanota and the Nevado Verónica in the background. The type locality of *Gastrotheca ochoai* is the base of the cliff at the left of the picture; *Gastrotheca marsupiata* occurs on the valley floor in the foreground.



FIG. 11. Type locality of *Gastrotheca ochoai* showing bromeliads of the face of the cliff.



FIG. 12. Adult *Gastrotheca ochoai* in bromeliad at type locality.

of *G. marsupiata*; the dry páramo in the upper Río Paucartambo valley inhabited by *G. marsupiata* contrasts markedly with the adjacent humid crest of the Amazonian rim where *G. excubitor* is found. Adult females of *G. excubitor* have few, large ovarian

eggs, indicating that prolonged development of young or completion of metamorphosis in the pouch is to be expected in this species. This reproductive mode contrasts with that of *G. marsupiata*.

Gastrotheca marsupiata, *peruana*, and *griswoldi* commonly occur in wet and dry páramo. Frequently they are found under rocks or near small seeps or streams. Young of *G. griswoldi* are known to complete metamorphosis within the maternal pouch, whereas in *G. peruana*, like *G. marsupiata*, development includes a free-swimming tadpole stage. *Gastrotheca griswoldi* occupies geographically and altitudinally intermediate areas between *G. marsupiata* (lower elevations) and *G. peruana* (higher elevations) in the upper Río Mantaro valley.

The geographically close populations of *G. christiani* and *G. gracilis* also differ in reproductive modes (R. F. Laurent, pers. com.). The young of the former undergo metamorphosis within the maternal pouch, whereas the latter has free-swimming tadpoles. Thus, in the *Gastrotheca marsupiata* group sympatric species or species living in geographic proximity differ from one another in reproductive mode. Selection for different reproductive strategies would result in reducing competition for limited resources, in this case aquatic situations for larval development.

The complex color polymorphism observed in populations of *G. marsupiata* and *G. peruana* (and also in *G. riobambae* in Ecuador) remain to be investigated from an evolutionary point of view. Jameson and Pequegnat (1971) showed that a similar polymorphism in *Hyla regilla* was correlated with seasonal and microecological differences in vegetation color.

RESUMEN

La revisión de las ranas del género *Gastrotheca* encontradas en los Andes al sur de la depresión de Huancabamba al norte del Perú, indica la presencia de siete especies. Catorce nombres triviales han sido aplicados a cinco de estas especies; además aquí se nombran dos especies adicionales (Table 1). *Gastrotheca peruana*, *G. griswoldi* y *G. marsupiata* son especies alopátricas que se encuentran en el norte del Perú, en el centro del Perú, y en el sur del Perú hasta Bolivia respectivamente. Las dos nuevas especies, *G. exenbitor* y *G. ochoai*, se encuentran en la cuesta oriental andina, y en los valles amazónicos y interandinos del sur del Perú respectivamente. Dos especies, *G. gracilis* y *G. christiani* habitan las cuestas orientales andinas en el norte de Argentina.

Las poblaciones Ecuatorianas anteriormente llamadas *G. mar-*

supiata no son coespecíficas con la verdadera *G. marsupiata* del sur del Perú. *Gastrotheca riobambae* (Fowler, 1913) fué el primer nombre que se aplicó a las poblaciones Ecuatorianas; *Hyla quitoe* Fowler, 1913, *Chorophilus olivaceus* Andersson, 1945, y *Gastrotheca marsupiata ecuatoriensis* Vellard, 1957, son otros sinónimos dados más tarde.

Gastrotheca marsupiata, *peruana*, y *gracilis* tienen renacuajos de vida libre, mientras que en las otras especies su desarrollo es completamente dentro de la bolsa maternal. Las especies que habitan en simpátria o en regiones geográficas muy cercanas difieren en las formas de reproducción.

SPECIMENS EXAMINED

Gastrotheca christiani

ARGENTINA: *Jujuy*: Alto calilegua, 2600 m, IML 1606; Río Las Lozas, KU 147306.

Gastrotheca excubitor

PERÚ: *Cuzco*: Abra Acanacu, 3520 m, IML 2014, KU 139199-201, UMMZ 131676; north slope Abra Acanacu, 3270-3400 m, KU 139193-8, 139449.

Gastrotheca gracilis

ARGENTINA: *Catamarca*: La Banderita, IML 1530 (5), KU 147307-8.

Gastrotheca griswoldi

PERÚ: *Huánuco*: ? Huánuco, MJP 494 (6). *Junín*: Casca, MCZ 22862-6, 81750-7; Comas, KU 138222-32, 138813-21; Hacienda Pucara, 8 km. E Morococha, MCZ 24400; Huasi, MCZ 24387-9, 81758-67; Huayhuay, MCZ 24390-2, 81768-72; Jachahuanca, MCZ 24418-9, 81705-49; La Oroya, AMNH 38572-6; Maraynioc, KU 137583-7, MCZ 241102-6, MNHN 8662 (5), UMMZ 90169 (3); Mayopampa, 2 km N La Oroya, KU 138221; Minas Janchiscochas, 40 km N Juajua, MCZ 22875-6; Paccha, 9.5 km NW La Oroya, IML 1702 (2), KU 139140-51, MJP 129 (3), 260 (13), 474; Pomamarca, UMMZ 122440; Tarma, MJP 205 (3). *Pasco*: Paucartambo, MJP 495 (6); 14 km SW Paucartambo, KU 139152-4, 139191-2, 139441.

Gastrotheca marsupiata

BOLIVIA: No specific locality, NHMW 16496.1-2; "Chaco," RMNH 4497. *Chiquisaca*: Sucre, MCZ 2576, 81773-4, SMF 30697. *Cochabamba*: No specific locality, UMMZ 66637 (7), 66638 (6); Cochabamba, ZSM 17/1949 (7), 24/1962 (9); Cochabamba Valley, UMMZ 68165 (2); Incachaca, AMNH 34033; Puerto de San Mateo, NHMW 16490, 16491 (5); Tarata, Yungas del Chapare, UMMZ 68164; "Yungas," BMNH 95.11.21.50; Yungas de Totora-Monte Punco, KU 125374-5. *La Paz*: Choro, AMNH 3151, 10565-8, BMNH 1902.5.29.147-54, NHMW 6486.1-3; Tiquina, MJP 177 (4), MNHN 57/864; Totara, MCZ 15334, 15581, 15585-6, UMMZ 92268. *Potosí*: Potosí, BMNH 1902.5.29.155; Tupiza, ZSM 293/1929; 25 km NE Villagren, MVZ 65531.

PERÚ: No specific locality, MCZ 4994-8; Kalinourhin, NHMW 18440 (3). *Apurímac*: Andahuaylas, CAS 84778. *Ayacucho*: Puquio, MJP 470; Querobamba, SMF 33816. *Cuzco*: 10 km E Abra Huilque, KU 138252-9; Chilca, 10 km NW Ollantaytambo, KU 138374-92, 138765-6 (tadpoles), 139186, 139446 (tadpoles), 139447 (young), UMMZ 130156; Cuzco, IML 1701 (2), 2013 (3), KU 138368-9, MCZ 4173-4, MJP 124, MNHN 4877,

NHMH 6484, USNM 49559-60; 4 km NW Cuzco, KU 138334-67, 138372-3 (skeletons), 138767 (tadpoles); 3 km W Cuzco, KU 138370-1; 1 km S Cuzco, KU 139184; Granja de la Raya, KU 138319-33; Huaracundo, USNM 60766-8; La Toma, MJP 786, 788 (2); Oropeza, KU 138393-6, 138768 (tadpoles); 14.5 km SW Paucartambo, KU 139187-8; San Jerónimo, 10.7 km ESE Cuzco, KU 139155-83, 139442-5 (tadpoles); Sicuani, KU 138307-18; Tambomachay, 5 km N Cuzco, KU 139185; Tincochchaca, USNM 49561-3; Teco-poqueyu, MCZ 5059, USNM 60753-4; Tres Cruces, 18 km N Paucartambo, MVZ 57804; Urubamba, KU 138397-8, MJP 767; Uvini, Río Cosireni, MCZ 5343, USNM 60769. *Huancavelica*: Conaica, MJP 345; Churcampa, MJP 239; Lircay, KU 138260; 15 km W Lircay, KU 138291-4, 138295-6 (skeletons); 20 km W Lircay, KU 138261-90; Huancavelica, KU 138297-306, 138399-400; Pampas, KU 138243-4, 138764 (tadpoles); 20 km W Pampas, KU 138245-51. *Junín*: Acolla, MJP 397, 449 (2); "Camino a Socorro," MJP 787, 790 (2); Hacienda Yanamarca, MJP 314 (3); Huancayo, MJP 189, 201; Pachacayo, MJP 55 (2); Santa Rosa de Ocopa, KU 138242, MJP 818; Tragadiro, MJP 795. *Puno*: No specific locality, MJP 168; Capachica, BMNH 1940.4.10.21-9; Ilave, MJP 227; Moho, MJP 172, 232; Pucará, BMNH 1904.10.26.78-9, NHMW 6486.4; Puno, MJP 167, 231, 779, 782 (11); San Antón, BMNH 1907.5.7.37-8.

Gastrotheca ochoai

PERÚ: Cuzco: Chilca, 10 km NW Ollantaytambo, IML 2012, KU 138628-65, 139202-9, 139210-11 (skeletons), 139448, UMMZ 131688 (9); 3 km SSW Pilahuata, MNSAA (4). *Puno*: Ollachea, 53 km N Macusani, KU 138666-718.

Gastrotheca peruana

PERÚ: Ancash: Caras, BMNH 1900.6.20.46-50; Chavin de Huantar, KU 138514-26; Chiquian, KU 138495-512, 138770 (tadpoles); Huaráz, KU 138513, MCZ 24542; 5 km N Recuay, KU 138527-44, 138771 (tadpoles). *Cajamarca*: Cajamarca, KU 138494, MJP 478 (4), MNHN 57/863; Cutervo, MJP 264 (tadpoles), 269. *Huánuco*: 5 km NE La Unión, KU 138411-52, 138772 (tadpoles). *Junín*: Añascancha, MJP 228; Casa Pata, MJP 318, 341; between Casa Pata and Añascancha, KU 139189-90; Lago Junín, BMNH 1940.2.25.30. *La Libertad*: Huamachuco, KU 138453-9, MJP 245 (47), 762 (4); Laguna Sacasacocha, 12 km E Huamachuco, IML 1703, KU 138460-90, 138492-3 (skeletons); Otuzco, KU 138545-6; Pomacocha, MJP 637 (3); Tayabamba, MJP 637 (3 + tadpoles), 759 (tadpoles). *Pasco*: Km 37 between Carhuamayo and Paucartambo, MJP 459 (2); Huayllay, MJP 758 (2); Lago de Pumrún, MJP 191 (2), 195; Mina San José, Huarón, MJP 446.

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